

A re-evaluation of Straneck's (1993) data on the taxonomic status of *Serpophaga subcristata* and *S. munda* (Passeriformes: Tyrannidae): conspecifics or semispecies?

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In 1993, R. J. Straneck published a paper entitled "Aportes para la unificación de *Serpophaga subcristata* y *Serpophaga munda*, y la revalidación de *Serpophaga griseiceps* (Aves: Tyrannidae)". As the title implies, Straneck concluded, based on field and museum studies, that the first two taxa are conspecific and that a third, often misidentified and specifically distinct taxon exists, namely Grey-crowned Tyrannulet *S. griseiceps*. However, as I will discuss in this paper, the article contains several methodological flaws, and a careful re-examination of the presented data using objective, quantitative and conservative criteria (Isler *et al.* 1997, 1998, 1999) must actually reach the opposite conclusion, namely that given the current knowledge, White-crested Tyrannulet *S. subcristata* and White-bellied Tyrannulet *S. munda* are valid biological species. I have field experience with both forms, but the present paper is based solely on Straneck's (1993) account. The situation of *S. griseiceps* is less straightforward (e.g., Traylor 1982 considered the type specimens of *S. griseiceps* as juveniles of *S. munda*) and will be treated separately. Because Straneck's (1993) conclusions have already been adopted by at least three recent publications (de la Peña & Rumboll 1998, Mayer 2000, Mezquida & Marone 2000), a word of caution regarding his paper seems timely.

The genus *Serpophaga* contains five currently recognised species (Monroe & Sibley 1993, Ridgely & Tudor 1994), including *subcristata* and *munda*. Of the remaining three species, one is restricted to river islands of the Amazon and Orinoco systems and two are closely associated with water in the northern to central Andes and south-eastern South America, respectively (Ridgely & Tudor 1994). *S. subcristata* and *S. munda* are restricted to the southern half of the continent and show a basically parapatric distribution pattern, at least during the breeding season (Ridgely & Tudor 1994). Whereas *subcristata* is widely distributed in forest, woodland and scrub of south-eastern South America with its western limit in the Andean foothills, *munda* occurs in the eastern Andes from foothills up to about 3,000 m (in Cochabamba, Bolivia; J. A. Balderrama and S. K. Herzog, unpubl. data) in deciduous scrub and forest during the austral summer. In the austral winter, latitudinal and possibly altitudinal migrants are found in the lowlands (chaco) east of the Andean breeding grounds and well within the range of *S. subcristata* (Fjeldså & Krabbe 1990, Ridgely & Tudor 1994, Chesser 1997).

The notion that the two taxa may be conspecific is not new (e.g., Zimmer 1955). However, rather than presenting a review of the older accounts on the topic, I re-evaluate the new data from Argentina published by Straneck (1993). Because that paper appeared in a relatively inaccessible journal, I will briefly summarise its content and point out major shortcomings in the appropriate places.

Distribution

Field observations and specimen collections were made during eight years (actual time period not stated) in ten provinces of northern and central Argentina (south to La Pampa and Buenos Aires; mainly austral spring to summer, year-round in four provinces) and supplemented with specimen examinations in four Argentinian museums. A map with the breeding distribution is presented, showing *munda* restricted to the western and *subcristata* to the eastern half of northern and central Argentina, which largely coincides with Ridgely & Tudor (1994) (except that no specimen records are shown south of La Pampa). Populations of both taxa are stated to be partially migratory. Whereas no overlap in the breeding ranges of the two taxa is evident, Straneck reported individuals intermediate between *subcristata* and *munda* from five localities in the contact zone of their respective ranges. However, no additional information is given on whether any hybrids were collected, how they differed from typical *subcristata* or *munda* and the frequency with which hybrids were observed at the five sites, i.e., whether a narrow but defined hybrid zone exists (which would render the two forms megasubspecies of *S. subcristata*) or if gene flow between both populations occurs at only a low and local level (hybridization paraptry *sensu* Haffer 1992).

Vocalizations and playback experiments

Thirty-eight individuals of both *subcristata* and *munda* were tape-recorded and 875 of their vocalizations analysed qualitatively. Sonograms of the four most common vocalizations of each taxon (without locality data) illustrate the main result, namely that “vocal differences between both forms are minimal and attributable only to individual or regional differences.” My main criticism here is that Straneck’s judgements were purely qualitative and that a careful examination of possible differences in specific vocal characters, including quantitative analysis, is required before any decision regarding species limits can be made (*cf.* Isler *et al.* 1998). This point is exemplified by well-known North American superspecies of small tyrannids such as the one composed of *Empidonax traillii* and *E. alnorum*, which are considered valid species (AOU 1998) despite only subtle vocal differences between them. To avoid confusion, it should be noted that Straneck considered J. V. Remsen’s (Remsen & Taylor 1989: 54) description of the song of *subcristata* to be erroneous and referable to *S. griseiceps*, the taxon Straneck intended to revalidate. New field evidence (*cf.* recordings by the author and others in Mayer 2000) appears to corroborate Straneck’s point of view.

Additionally, Straneck conducted playback experiments (five each) in the breeding season to test for territorial responses, playing vocalizations of *subcristata* to *munda* and vice versa (although without specifying the detailed methodology and again without locality data). Reactions of all test birds were positive, i.e., they showed a strong behavioural response to the playback. However, positive responses to playback in nature are not as straightforward and unequivocal as they may seem. A number of antbird (Thamnophilidae) species, including sympatric species, such as *Thamnophilus antshrikes*, have been found to respond to each other's song, a behaviour possibly related to interspecific territoriality (M. Isler, pers. comm.). J. Goerck (pers. comm.) observed a similar behaviour in *Drymophila* antbirds. Because interspecific territoriality might also be operating in the case of *subcristata* and *munda*, playback experiments need to be designed (cf. Kroodsma 1989a) and interpreted carefully, and a positive response (as opposed to a lack of response) is of limited value for resolving taxonomic questions.

External morphology

The known and obvious differences in plumage colouration between the two taxa (Ridgely & Tudor 1994) are mentioned briefly, and morphometric data are presented for 40 individuals of *subcristata* and 12 of *munda*; whether measurements were taken from specimens or live birds is not stated. Unfortunately, no clear conclusion can be drawn from these data by the reader (and Straneck makes no attempt to do so either) since only mean values for each of the seven measurements are given, lacking standard deviations and ranges. Also, only body mass was calculated separately for males and females, but sample sizes for each sex were not given. Differences between mean values of each taxon are minimal (<0.5 mm or g) except for tail length (2.0 mm longer in *subcristata*) and wingspan (2.8 mm wider in *munda*). The shorter tail in *munda* is contradictory to both Zimmer (1955) and Bó (1969), who found male *munda* to be longer-tailed than male *subcristata*, although with slight overlap in measurement ranges. Zimmer (1955) noted that the difference in tail length between the two taxa is less pronounced in females than it is in males; therefore, Straneck's failure to present all morphometric data separated by sex may well explain his unexpected tail measurements.

What do Straneck's data really tell us?

Straneck concluded that, based on identical vocalizations and despite differences in plumage colouration, *S. subcristata* and *S. munda* must be considered conspecific. Neither the similar measurements nor the existence of hybrids are mentioned or discussed any further, although these must certainly have influenced the author's decision. Recent pioneering studies on species limits in another family of suboscine birds (Thamnophilidae) (Isler *et al.* 1997, 1998, 1999), which likewise focused on vocalizations and external morphology, have developed objective criteria for establishing species limits in that family. Because the development of these criteria

was initially derived from the convincing evidence that vocalizations in the family Tyrannidae are entirely innate (Kroodsma 1984, 1985, 1989b; Kroodsma & Konishi 1991), it is logical to apply the same criteria to species-level taxonomy of tyrant flycatchers.

Isler *et al.* (1999) treat parapatric populations as valid species if they are “diagnosable by *either* morphology or vocalizations and with a lack of clinal intermediacy at the contact zone indicating that gene flow is absent or highly restricted.” In contrast, adjacent populations diagnosable by either morphology or vocalizations that have a contact zone where “intermediates occur in a steep, apparently stable cline” are treated as subspecies. These criteria illustrate the importance of the degree of gene flow and the geographic distribution of hybridization for determining species limits in adjacent populations of suboscines, to which Straneck pays only minimal attention. Because his data are not explicit, taking a conservative approach one must assume that intermediate individuals occur only locally and gene flow between both taxa is indeed highly restricted. Applying the above criteria, *subcristata* and *munda* must thus be considered valid species (semispecies, i.e., taxa that replace each other geographically with only limited hybridization in the area of contact; Haffer 1992).

The need to collect additional information is particularly relevant in view of several recent publications (e.g., Bierregaard *et al.* 1997, Zimmer *et al.* 2001) documenting the existence of cryptic biological species that had been overlooked due to the lack of data from contact zones between geographically representative forms. Whereas a detailed field study quantifying the extent of hybridization between *subcristata* and *munda* together with an appropriate analysis of vocal and morphometric characteristics may prove them to be conspecific, for the time being they are better treated as separate species.

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